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Predation risk and resource availability explain roost locations of Whimbrel *Numenius phaeopus* in a tropical mangrove delta

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Roosts are important sites for shorebirds in non-breeding areas at night and during high tides. How the spatial configuration of food and risk of predation and disturbance influence roost site use in tropical locations remains poorly known. We analysed the locations of nocturnal roosts of Whimbrel *Numenius phaeopus* in mangroves of Sanquianga National Park, Colombia, with respect to variation in spatial variables related to food resources and risk of predation and disturbance. We contrasted characteristics of all 13 known nocturnal roost locations with those of all other mangrove islands ($n = 209$) within the limits of the park. We estimated the distance from roosts and other mangrove islands to foraging sites, and sources of predators and human disturbance. Larger areas of feeding habitat surrounded nocturnal roosts than other mangrove islands, and the average distance to individual feeding patches was shorter. Roosts were also more isolated than other islands, but proximity to sources of human disturbance did not differ. We conclude that Whimbrel roost site use in Sanquianga was best explained by a combination of access to feeding territories and isolation from potential sources of mainland predators, but not by avoidance of human disturbance. Beyond identifying factors influencing roost site selection, the large aggregations of individuals in single locations may suggest that presence of conspecifics itself also plays a role in the formation of Whimbrel roosts. We highlight the interaction of food and risk landscapes with intraspecific attraction on the roost site selection by Whimbrels and the importance of mangroves as roosting sites in tropical regions.

Keywords: Colombia, habitat selection, mangroves, predation avoidance.

Communal roosting is a widespread behaviour within birds and social mammals (Beauchamp 1999, 2014). Three general explanations have been proposed for communal bird roosts: thermoregulatory benefits, greater foraging efficiency and protection from predation (Ydenberg & Prins 1984). Roosting with companions can provide protection against extreme weather and reduce energetic costs associated with thermoregulation (Yom-Tov *et al.* 1977, Du Plessis & Williams 1994, Rehfisch *et al.* 2003, Burton & Evans 2008, Williams & Du Plessis 2013). Roosts can also increase foraging efficiency through information transfer (Ward & Zahavi 1972), recruitment of foragers at the roost (Burton *et al.* 1996) or attraction of conspecifics to food sources (Buckley 1996). Roosting with companions can improve predator detection and dilute individual predation risk (Eiserer 1984) and can offer a safety buffer to birds roosting at the centre of the flock (Weatherhead 1983). These explanations highlight the social value of roosting with conspecifics, but an alternative fourth

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explanation is that communal roosts are coincidental aggregations of individuals searching independently for roost sites with similar characteristics (Beauchamp 1999).

Comparing the habitat features of roosts and other locations may shed light on the relative importance of competing explanations for roost site formation in birds. Studies using this approach have demonstrated that birds may aggregate near foraging patches (Caccamise & Morrison 1988), at sites offering safety from predators (Rosa *et al.* 2006) or lower levels of disturbance (Peters & Otis 2007). On the other hand, roosts are not static. Conklin *et al.* (2008) argued that Pacific Dunlin *Calidris alpina* constantly shifted between a wide suite of readily available roost sites in part to avoid predators. Habitat features of roosts may also provide shelter against cold winds (Colwell & Sundeen 2000, Peters & Otis 2007) or extreme heat conditions (Rogers *et al.* 2006a).

Most migrant and non-breeding shorebirds typically roost at night but also may aggregate when foraging areas are covered by high tides during the day. When high tide limits the availability of roosts safe from diurnal predators, small shorebirds can take to extremes, making hour-long overwater flights rather than land flights (Ydenberg *et al.* 2010). It has been suggested that the availability of sites offering favourable characteristics can constrain the location of both nocturnal and high-tide roosts of shorebirds (Rogers *et al.* 2006b, but see Conklin *et al.* 2008). The time or energetic costs of travelling between roosts and feeding areas could therefore constrain shorebird distributions (Rehfisch *et al.* 1996, 2003). On the one hand, individuals may prefer to use roost sites closer to their feeding territories. However, with respect to safety, shorebirds might choose roosting sites with features that prevent or impede predator attacks. For example, to reduce the risk of surprise attacks from raptors, shorebirds may favour roosting on open mudflats far from vegetation (Piersma *et al.* 2006, Rosa *et al.* 2006). Shorebirds are more vulnerable to predation by mammals when close to vegetation or at roosts that are not isolated (Hockey 1985). The availability of roosts safe from terrestrial predators could constrain the distribution of non-breeding shorebirds (Rogers *et al.* 2006a).

Human activity can incur high energetic costs for roosting shorebirds (Rogers *et al.* 2006b), impact the choice of roosting habitats (Yasué 2006) and have long-term effects on the use and abandonment of roosting sites (Burton *et al.* 1996, Colwell & Sundeen 2000, Peters & Otis 2006). To understand fully the influence of feeding areas, predator risk and disturbance on roost selection by non-breeding shorebirds, further work is necessary on the spatial distribution of shorebird roosts in relation to sources and types of potential predators in non-breeding areas, particularly in tropical habitats.

Mangroves are widespread habitats in tropical regions across shorebird flyways (Butler *et al.* 2001, Bamford *et al.* 2008). Mangroves are strong predictors of feeding habitat productivity and high shorebird densities at global and regional scales (Butler *et al.* 1997, 2001). Aside from feeding, mangroves provide roosting habitat for several species of shorebirds, in particular for the Whimbrel *Numenius phaeopus* (Johnston-González *et al.* 2006, Zharikov & Milton 2009). This study focuses on the use of mangroves as roost sites for the Whimbrel in Sanquianga National Park, along the southern Pacific coast of Colombia (Fig. 1). This large tropical river delta covers ~ 480 km^2, including barrier islands and sand spits along 60 km of coastline and ~ 200 mangrove islands, providing many potential locations for feeding and roosting shorebirds.

In Sanquianga, as in other non-breeding locations (Skeel & Mallory 1996), Whimbrels occupy individually defended diurnal foraging territories (Ruiz-Guerra 2004). Those territories are widely dispersed throughout the entire delta (Anchico *et al.* 2015). Typically, birds arrive at their foraging territories as tide recedes after dawn and they move into adjacent mangroves, grass and beaches during diurnal high tides (Abril 2011). On rising evening tides, they leave these territories and congregate at a small number of nocturnal roost sites (Hevia 2011). Roosts are established on mangrove islands, where Whimbrels perch on top of roots and lower branches of Red Mangrove *Rhizophora mangle*, the most common mangrove species within the delta (Abril 2011, Hevia 2011). To date, only 13 Whimbrel roost sites have been identified in the study area and up to 3500–4000 individuals, constituting 55–60% of the local population, may aggregate at a single roost site (Johnston-González *et al.* 2006, Abril 2011, Hevia 2011). Many individuals thus make lengthy daily commutes of several kilometres, raising the question of why some Whimbrels in Sanquianga make daily commutes to a distant roost that are more

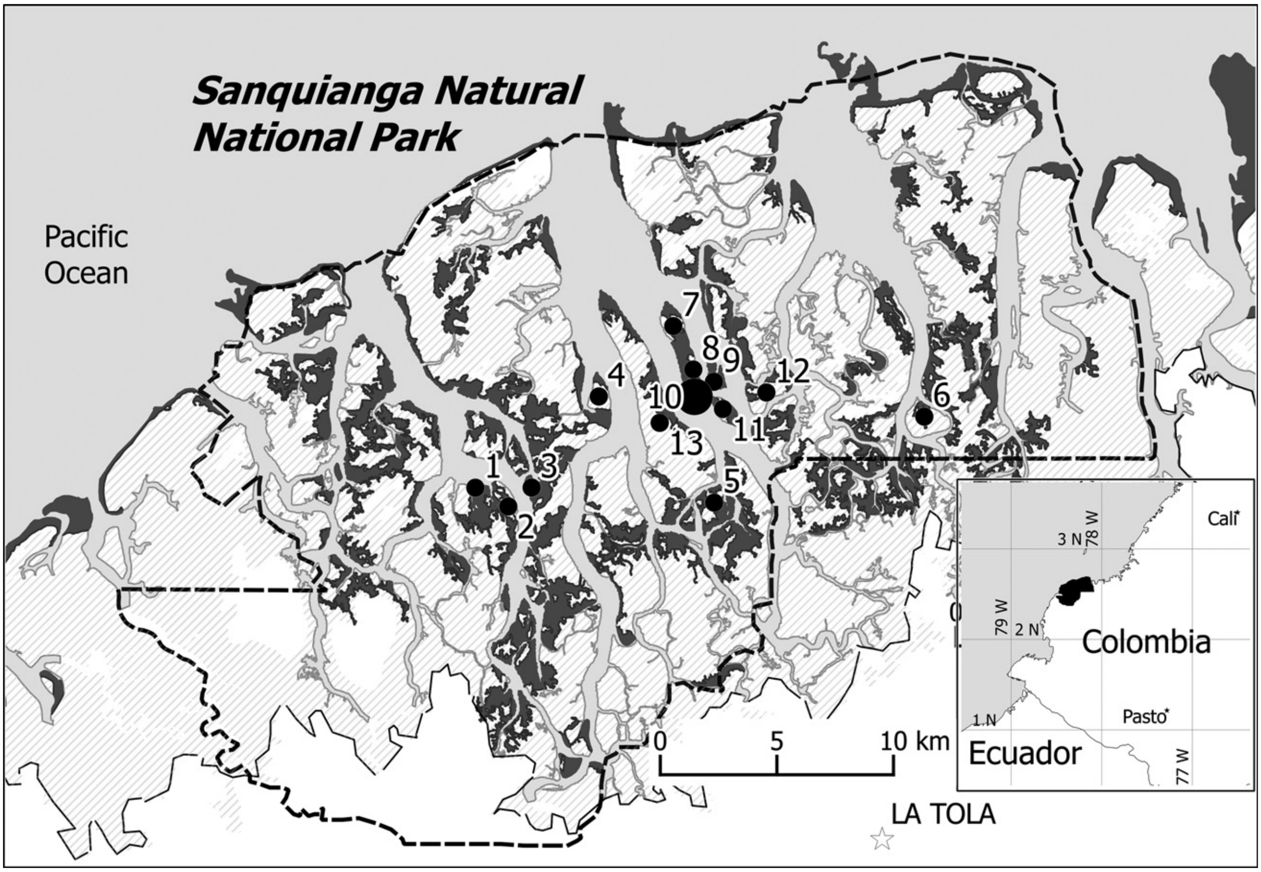

Figure 1. Whimbrel roosts (black dots) in Sanquianga National Park (dashed line), Colombia. The main roost is indicated by a large circle. Mudflats are shown in dark grey, mangroves with a diagonal grey pattern and emerged lands in white. The mainland extends below the broken lines at the bottom of the map. (1) Isla Cocal, (2) Campo Alegre, (3) Conguero, (4) Punta Isla Grande, (5) Estero El Carmen, (6) Aguacatal, (7-13) 'El Parguero' (see Table S1 for details).

expensive in time and energy than roosting closer to their feeding territories, as many do by day.

In this study, we tested predictions from hypotheses for nocturnal roost site choice in relation to spatial variables that can be related to the distribution of food resources, predation risk and human disturbance. If the distribution of feeding locations affects that of roosting sites, occupied Whimbrel roosts should be more centrally located relative to larger areas of feeding substrate than other potential roost sites, thereby allowing average distances to feeding territories to be shorter. On the other hand, if roost use is a strategy to reduce predation risk, the locations of occupied roosts, relative to other potential roost sites, should reflect avoidance of sources of potential predators. Finally, if human disturbance plays a role, we predict that occupied roost sites will be more distant than other potential roost sites from human villages and aquatic transportation routes. In summary, we expect that Whimbrels occupy roosting sites close to sources of feeding habitat and far from sources of predation risk and disturbance.

METHODS

Study area

Sanquianga National Park lies on the estuary of the Sanquianga and the diverted Patía rivers (Parra & Ángel 2014), on the southern portion of the Colombian Pacific coast (Fig. 1; 2.5°N, 78.3°W). The park comprises 80 000 ha of coastal habitats, including mangroves (48%), extensive mudflats (15%) and estuarine waters along four major basins. A semi-diurnal tidal regime immerses much of the area in saline/brackish waters twice daily (IDEAM 2016). Shorebird habitat is widely distributed, with hundreds of mangrove islands and mudflat patches interspersed across thousands of kilometres of tidal channels. Forests other than mangrove, crops and human settlement are restricted to islands with lands above the tidal influence (non-flooded) and the mainland in the southern end of the Park. Together with sandy beaches, these habitats occupy only 4–6% of the park (UAESPNN 2010). The delta lacks road access, and the shallow waters and marked tidal regimen limits cargo transport by water. As a result of its inaccessibility and the designation as a National Park and Afro-Colombian collective territories (UAESPNN 2005), there is no large-scale industrial, urban or tourism development within the park. Human population is very sparse, averaging 8 inhabitants/km², concentrated around major villages. Nevertheless, approximately 10 000 inhabitants live within the park, and a further 20 000 live in surrounding municipalities (UAESPNN 2005). People obtain food and materials for fuel and shelter from the park, and there are artisanal fisheries for shrimp, estuarine fishes and mangrove cockles. Medium-sized vessels and small boats for personal transport are common on the major waterways (UAESPNN 2005).

Sanquianga NP holds one of the largest concentrations of non-breeding Whimbrels in northern South America (Wilke & Johnston-González 2010). Between 6800 and 8000 birds, making up 8–10% of the continental population (Andres *et al.* 2012), are estimated to winter in Sanquianga (Johnston-González & Eusse-González 2009). As elsewhere in the non-breeding range, Whimbrels establish feeding territories that are maintained throughout the non-breeding season (Skeel & Mallory 1996). In Sanquianga these feeding territories cover on average 2.2–2.8 ha, predominantly in mudflats (Abril 2011) but occasionally in pasture or on sandy beaches (Ruiz-Guerra 2004, Hevia 2011).

Identifying roosting locations

Roost locations and the maximum number of Whimbrels recorded at each roost were pooled from Ruiz-Guerra (2004), Abril (2011), Hevia (2011) and during additional visits made by R.J.G. between 2009 and 2014 (Supporting Information Table S1). ‘Islerias’, the main roosting location, was originally identified by Park rangers and local fishermen in 2006 and was described as containing ~ 1000 individuals (Johnston-González *et al.* 2006). Later surveys revealed that more than half of Sanquianga’s Whimbrels (3500–4000 individuals) often gather at this site (Hevia 2011). A satellite-tagged individual (L. Tibbits pers. comm.) revealed the location of a second roost containing about 200 individuals, and other small roost sites with fewer than 100 individuals were identified during the winters of 2007–2008 (Abril 2011) and 2009 and 2012–2014 (R. Johnston-Gonzalez pers. obs.). The largest and second largest roosts have been consistently used to date but we lack evidence for occupancy of the others. All such observations were completed within the 2 h prior to sunset when Whimbrels leave their feeding territories and gather in flocks before approaching their roosts. For each site we made efforts to remain as close as possible to sunset and assumed the roost will be used at night. Given safety concerns, we did not attempt to remain at night. We considered as a nocturnal roost, the recorded use of an island by at least four individuals within this time. Using these opportunistic observations, we gathered information for 13 ‘occupied roosts’ or mangrove islands with evidence of roost use by Whimbrels, covering 70–80% of the local Whimbrel population. There is scope to find other roosts, but a complete survey of potential roost sites seemed impossible, given safety and logistical restrictions to cover > 80 000 ha of mangroves within only a 2-h window before sunset. The other 209 available islands were considered ‘potential roosts’ for which we lack evidence of Whimbrel use, but were not systematically searched.

We used digital cartography at 1 : 100 000 (UAESPNN 2005) and 1 : 500 000 (IDEAM *et al.* 2007) and several tools from the QGIS software (QGIS Development Team 2016) to extract spatial attributes of occupied and potential roost sites and their surrounding habitat covers. We used the ‘mean coordinates tool’ to calculate the centres of each mangrove island (occupied and potential) and ‘distance matrix tool’ and ‘variable distance buffer’ to estimate distances between them and other habitat covers using different radii or ‘buffers’. Below we describe those attributes in more detail.

Access to feeding sites and centrality

To determine whether roost location correlated with access to foraging sites, for each mangrove island (occupied and potential) we measured the proximity and amount of feeding habitat available. The Whimbrel uses sand beaches and artificial pastures within the study area, but the amount of those habitats in the Park (UAESPNN 2010) and bird density is marginal. In comparison, mudflats represent the main feeding habitat with respect to both the habitat area and the density of birds observed in that habitat (Abril 2011). We used habitat maps of the study area (IDEAM, IGAC, IAvH, Invemar, I.Sinchi & IIAP 2007, UAESPNN 2010) to identify mudflats. We overlapped and compared areas classified as mudflats with free satellite data from Google Earth, and confirmed that the map accurately represented mudflats near low tide. Using these habitat maps we were able to identify all mudflats of > 0.5 ha at low tide within the Park and in a 35-km radius of its limits. This distance is marginally larger than the maximum daily commute reported for other shorebird species (Rehfisch *et al.* 2003, Rogers *et al.* 2006b) and is thus expected to contain all foraging areas used by Whimbrels roosting within the park. Using this threshold, we included more than 11 000 ha of mudflats within the park (Fig. 1) and a further ~ 3000 ha surrounding it. We computed (1) distance to each mudflat within a 35-km radius of each mangrove island and (2) accumulated area of all potential feeding sites at incremental radii from 0 to 35 km of the centre of each mangrove island.

It is likely that many birds will fly shorter distances to roosts than the maximum of 35 km; therefore, to compare feeding habitat available around occupied and potential roosts we used an additional buffer at 12 km. We considered what the minimum buffer around an ideal roost would be, on which all birds would access feeding territories. As a reference we used the population estimated on the main roost (~ 3000 individuals, Hevia 2011) and 2.5 ha as the average size of feeding territories in the study area (Abril 2011). For all Whimbrels in the main roost to hold a feeding territory, ~ 7500 ha of mudflats will be required. This area was reached within a buffer ~ 12 km from the centre of the main roost and was chosen to compare with other occupied and potential roosts.

We also estimated whether roosts were centrally located in relation to major river basins or the entire study area. We extracted the geographical centre of each basin and of the entire study area from digital charts of the National Park, which match approximately the geography of the delta (UAESPNN 2010). We estimated the proximity of each roost to the centre of the nearest basin and to the centre of the study area to determine whether roosts were located centrally (close to the nearest basin centre) and in relation to the entire landscape (close to main centre) and compared those distances with all other potential roosts.

Isolation from terrestrial predators

Wintering shorebirds are prey of native and introduced terrestrial predators worldwide (Hays & Conant 2007, Geering *et al.* 2008, Colwell 2010, Aarif *et al.* 2014). Low-land forests in the study area harbour a diverse mammalian community including South American Raccoon *Procyon cancrivorus*, Ocelot *Leopardus pardalis* and Crab-eating Fox *Cerdocyon thous* (Asociación Calidris & Consejo Comunitario Esfuerzo Pescador Iscuande 2017). In addition to these medium-sized carnivores/omnivores, domestic and feral cats and dogs could potentially prey on shorebirds. We have no quantification of depredations by terrestrial predators on wintering shorebirds, but anecdotal evidence suggest that shorebirds avoid proximity to cats and dogs (Ruiz-Guerra 2004, R. Johnston-González pers. obs.) Most mangrove islands are below tidal level and unsuitable for habitation by terrestrial mammals; only the mainland in the southern border of the park and a dozen islands with sections above the tide level are likely to support terrestrial predator populations (Fig. 1). Using habitat maps of the study area (IDEAM, IGAC, IAvH, Invemar, I.Sinchi & IIAP 2007, UAESPNN 2010) we identified all 'non-flooded land', namely, non-flooded forest, open-vegetated areas and croplands as potential sources of terrestrial predators (Ruiz-Guerra *et al.* 2011, Asociación Calidris & Consejo Comunitario Esfuerzo Pescador Iscuandé 2017). We reasoned that locations farther from these sources would be less prone to incursion from terrestrial predators, as would islands with larger proportions of water surrounding them. For each island, we therefore calculated the distance to the nearest non-flooded land and to the mainland, and the proportion of mangrove vegetation versus water in a 1-km buffer around the island's centre.

Avoidance of human disturbance

Human disturbance (hereafter disturbance) can arise from the presence and activities of humans and their vehicles or pets (Robinson & Cranswick 2003). Disturbance can affect a range of shorebird behaviours (Frid & Dill 2002), including the use of roosting sites by shorebirds (Peters & Otis 2007). Whimbrels and other large shorebirds react strongly to the presence and proximity of disturbances by initiating escape responses (Weston *et al.* 2012). Proximity to sources of disturbance such as car or boat traffic has been used to quantify roost habitat selection (Burger *et al.* 2007, Conklin *et al.* 2008). For each island, we measured: (1) the distance from occupied and potential roost sites to the nearest village site; (2) the distance from occupied and potential roost sites to the nearest waterway used for transport; and (3) the human population density (km^2) within a 1-km radius.

Statistical analysis

We first determined whether values of feeding, isolation and disturbance variables differed between occupied (n = 13) and potential roost sites (n = 209). In the case of feeding areas, we tested for differences at multiple distances ('buffers') between 1 and 35 km, and we used fixed buffers for other variables. Visual inspection of frequency histograms and Mann–Whitney U-tests were used to examine univariate distributions; variables with overlapping distributions between occupied and potential roost sites were considered non-informative and were discarded. We then applied generalized linear models to evaluate how the presence of roost locations could be explained by a combination of the remaining habitat variables. We excluded variables that had similar means and distribution in the earlier univariate tests and, as the proportions of mangrove and water were highly correlated (r = –0.60), models included only one of these terms at a time. We evaluated the impact of linear terms because preliminary analysis found no evidence for non-linear relationships. The candidate set included three univariate models, three bivariate models and the null model (roost site use is not explained by a location of foraging sites, proximity to predators or disturbance). We evaluated the support for the six candidate models and selected the model with lowest Akaike's information criterion (AIC) and a delta value < 2 below other models. All statistical analyses were carried out in R software (R Core Team 2017).

RESULTS

Roost centrality and foraging habitat

Whimbrel nocturnal roosts occupy central locations within Sanquianga river basins, and half of them are clustered around the park's geographical centre (Fig. 1). Occupied roosts were located on average less than half the distance (5.4 km ± 2.91 sd) from the geographical centre of the park compared with potential roost sites (11.2 km ± 4.5 sd). Distances from occupied roost to the centre of their respective basin (3.51 km ± 1.67 sd) were slightly shorter but not significantly different from those for potential roost sites (5.6 km ± 3.00 sd) (Table 1). Between 7 and 22 km radii, there is up to 30% more area of mudflats surrounding occupied roosts than potential roost sites (Fig. 2). In the initial 7 km and after 22 km, average cumulative areas were similar between occupied and potential roost locations (Supporting Information Table S2). At 20 km, the mean distance from occupied roosts to potential feeding areas was 2.5 km shorter than that for potential roosting sites (Fig. 3b).

Avoiding human disturbance

The occupied Whimbrel roosts in Sanquianga did not differ from potential roost sites in terms of their average proximity to villages or human population (Table 1, Fig. 3d–f). Distance from the main roost to the nearest village was 2.52 km, only slightly farther than from smaller occupied roosts (2.12 km ± 1.26 sd) and potential roost sites (2.26 km ± 1.15 sd). As a result, most occupied roosts and potential roost sites have no permanent inhabitants within their immediate vicinity (1-km radius from its centre). Occupied roosts were at least 1 km away from major waterways used for human transportation (range 1–5.62 km) and the two largest roosts were even further away (2.85 km), but these differences were not statistically significant. These results do not support our prediction of greater distance to sources of disturbance in occupied roosts.

Isolation from terrestrial predators

Occupied roosts were at least 1.6 km from the nearest point of land, and 5 km from the mainland, located on small islands that lack emerged

Table 1. Habitat features of occupied Whimbrel roosts and other potential roosting sites in mangrove islands of Sanquianga National Park, Colombia.

	Occupied (*n* = 13)		Potential (*n* = 209)		Mann–Whitney test	
	Median	Min–Max	Median	Min–Max	U	*P*
General						
Size (ha)	57.46	4.7–1012.8	15.2	1.9–6131.4	774	0.150
Distance to centre of study area (km)	4.4	1.6–10.8	11.2	2.5–21.3	1821	< 0.001
Distance to centre of basin (km)	3.4	1.4–6.6	5.1	0.1–14.5	1434	0.060
Feeding						
Mudflat area, 12-km buffer (km²)	50.3	31.7–56.3	39.6	12.6–58.5	411	< 0.001
Average distance to mudflat, 12-km buffer (km)	7.5	6.1–8.1	7.2	6.1–9.2	847	0.284
Disturbance						
Distance to nearest village (km)	2.2	0.6–5.2	2.1	0.2–5.9	1074	0.946
Distance to nearest ship route (km)	2.9	1.0–5.6	3.7	0.3–13.1	1316.5	0.197
Human population 1-km buffer (No. of persons)	0.0	0–166	0.0	0–523	1122.5	0.634
Isolation						
% Water in 1-km buffer	48.3	17.4–71.4	25.1	0–74.9	420	< 0.001
% Mangrove in 1-km buffer	27.4	7.0–60.2	44	7.1–96.7	1534.5	0.017
Distance to mainland (km)	10.4	5.6–13.9	8.3	0.4–20.1	736	0.103
Distance to nearest land (km)	5.2	1.6–6.6	3.3	0.0–11.5	773	0.149

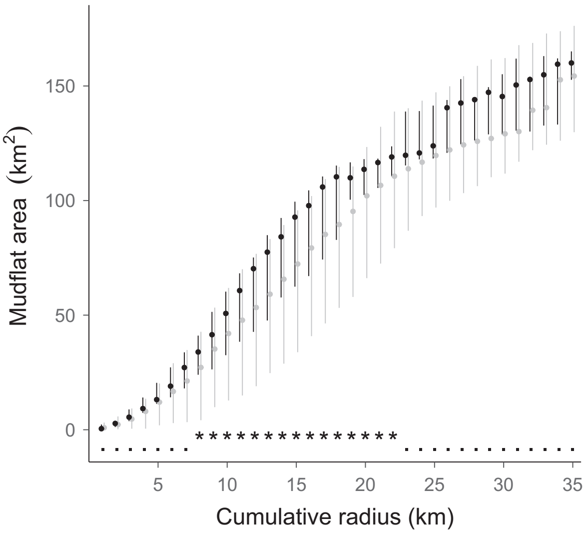

Figure 2. Mudflat area (km^2) accumulated on concentric 1-km buffers around occupied (black, *n* = 13) and potential roost sites (light grey, *n* = 209). Dots represent median values and lines the minimum and maximum values for each bin. Significant results of Wilcoxon tests at $P < 0.01$ are indicated with asterisks (see Table S2 for detailed results).

lands and are expected to be completely immersed by water at high tide, but those conditions were similar to those of potential roosts (Table 1, Fig. 4a–c & Fig. 4f). Occupied Whimbrel roosts were surrounded by more water and less mangrove forest than were potential roost sites (Table 1, Fig. 4d & Fig. 4e). Mangrove and shallow waters are the main habitats covering the park and are negatively correlated with each other ($r = -0.60$). The main roost was at the extreme of this continuum. Of all mangrove islands, this roost had the lowest proportion of mangrove (7%) and the third highest proportion of water (71%) within a 1-km radius of its centre (Supporting Information Fig. S1). Other occupied roosts were also among the most isolated locations (upper 10% of the distribution) and are surrounded by at least 50% water. The size of islands of occupied roosts did not differ from the size of potential roost sites.

Relative importance of predictors

The generalized linear model that included potential foraging area (within a 12-km radius) and the proportion of water (within a 1-km radius) was the most informative of the six models evaluated, accounting for 84% of cumulative weight of evidence, better than the next-best model by more than 4 AIC units (Table 2). Under this model, the odds of a mangrove island being used as a roost by Whimbrels increased 1.14 times (1.04–1.28; odds ratio of roost vs. non-roost) for every 1-km² increase in the area of mudflats, and by 2.5 times (1.86–5.85) for each 1% increase in the proportion of water surrounding the islands (Table 3, Fig. 5). Models based on only a single variable were

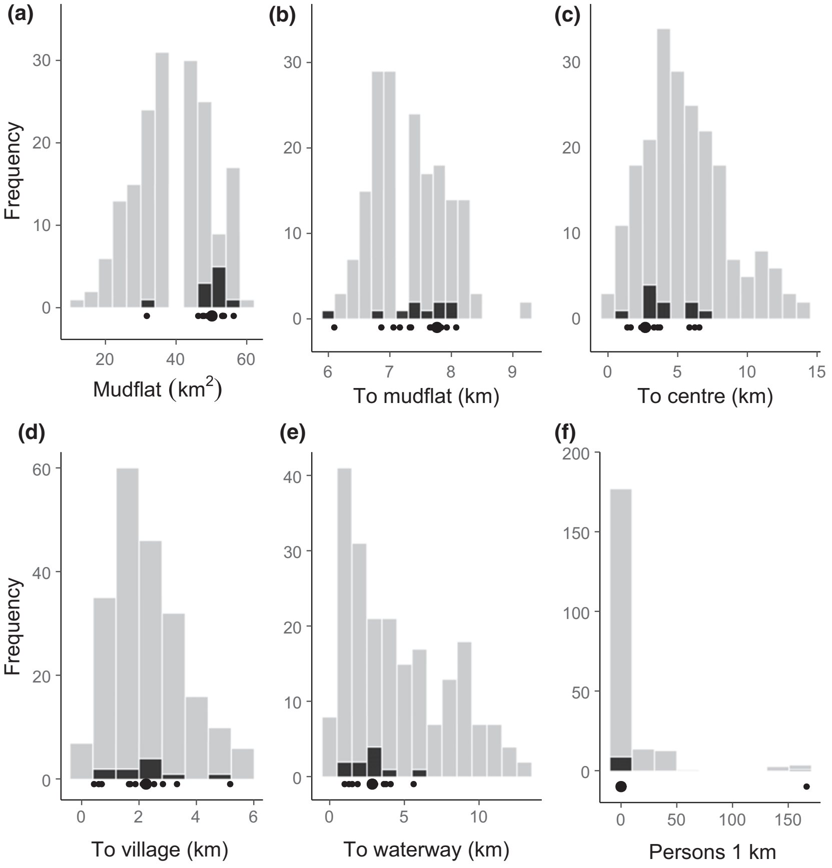

Figure 3. Frequency distribution of spatial attributes associated with access to feeding areas and human disturbance on occupied (black, $n = 13$) and potential roost sites (grey, $n = 209$) for Whimbrel in Sanquianga National Park. Black dots denote occupied roosts and the larger dot indicates the main roost. The height of the bar shows the number of islands within each bin. (a) Mudflat area (km^2) within a 12-km buffer, (b) average distance to mudflat (km^2) within a 12-km buffer, (c) distance to centre of basin (km), (d) distance to nearest village (km), (e) distance to nearest shipping route (km), and (f) human population within a 1-km buffer (number of persons).

uninformative, and all models performed better than the null model. Model selection including models with quadratic terms produced the same best model (analyses not shown). As explained in the Methods, 12 km was selected as the reference buffer, given this will contain a tidal flat area for 3000 individuals, the estimated population of the main roost. Although not evaluated, it is plausible that the area of tidal flats in other buffers within a 7- to 22-km range would give similar results if used as an explanatory variable.

DISCUSSION

Despite the hundreds of mangrove islands available in the study area, Whimbrels roosts were found in only a small number of them. Such roosts can gather a few dozen individuals or, in a unique case, hundreds to several thousand birds (Johnston-González *et al.* 2006, Abril 2011, Hevia 2011). Our opportunistic survey did not cover the entire Whimbrel population (70–80%), so there is scope for other roosts to be found. We found two strong independent predictors of Whimbrel roost location compared with other mangrove islands within the Sanquianga delta. Roost sites were closer to potential foraging sites and further away from potential sources of terrestrial predators. The largest roost and adjacent smaller roosts indeed occupy the most isolated island cluster in the delta. We found no evidence that roosting islands were different from other mangrove islands with respect to their distance to sources of human disturbance.

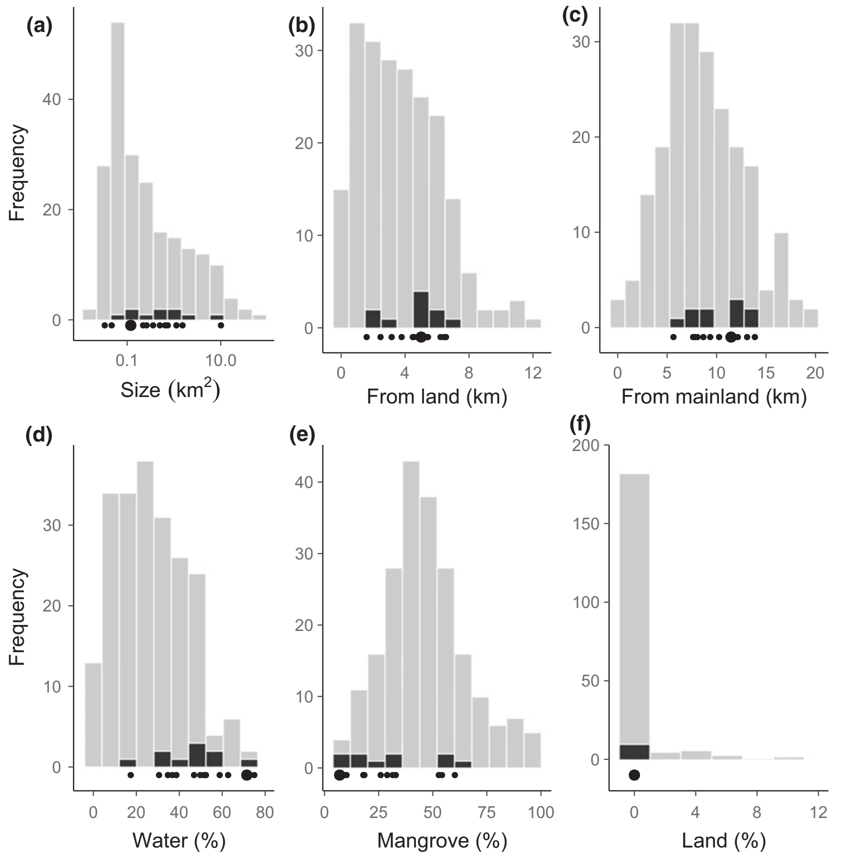

Figure 4. Frequency distribution of spatial attributes associated with isolation from predators on occupied (black, *n* = 13) and potential roost sites (grey, *n* = 209) for Whimbrel in Sanquianga National Park. Black dots denote occupied roosts and the larger dot indicates the main roost. The height of the bar shows the number of islands within each bin. (a) Island size (km^2), (b) distance to nearest land (km), (c) distance to mainland (km), (d) percentage of water (e) percentage of mangrove and (f) percentage of land within 1-km buffer.

Table 2. Generalized linear models with binomial error distribution and logit-link function explaining the location of Whimbrel roosts in Sanquianga National Park. The model including feeding area (within a 12-km radius) and percentage of water (1-km radius) was the most parsimonious in explaining the presence of Whimbrel roosts in mangrove islands.

Model	K	AICc	Δ AICc	AIC weight	Cumulative weight	Log likelihood
Feed Area12-km + %water 1-km	3	68.13	0	0.84	0.84	–31.01
Feed Area12-km + % mangrove 1-km	3	72.75	4.62	0.08	0.92	–33.32
Feed Area12-km	2	74.51	6.38	0.03	0.96	–35.23
% water 1-km	2	74.63	6.5	0.03	0.99	–35.29
% mangrove 1-km	2	77.57	9.44	0.01	1	–36.76
Null	1	83.56	15.44	0	1	–40.77

Foraging opportunities and patch-sitting hypothesis

We found support for our prediction that Whimbrel roost sites provide easier access to feeding areas compared with other islands. At intermediate distances (7–22 km), the area of mudflats available around roosts was up to 30% larger compared with other mangrove islands thought to be unused (Fig. 2). At the 12-km buffer, roosts averaged shorter distances to individual patches of mudflats (Fig. 3a & Fig. 3b). Both features (larger foraging

Table 3. Parameter estimates and upper and lower limits for 95% confidence intervals for coefficients in the best model of roost site selection by Whimbrel in Sanquianga National Park.

Variable	Estimate	Lower limit	Upper limit	Z statistic	*P*
Intercept	–12.631	–18.186	–7.076	–4.456	< 0.0001
Feeding area 12 km	0.156	0.054	0.259	2.983	0.0028
% water 1 km	7.430	3.407	11.453	3.620	0.0003

area and shorter distance to potential foraging sites) could explain why a large proportion of the local Whimbrel population aggregates in centrally located roosts. The mudflat area required for all 6800–8000 Whimbrels in the park to hold a feeding territory of ~ 2.5 ha is 18 500 ha. The mudflat area required for all Whimbrels estimated in the main roost (~ 3000 individuals, Hevia 2011) to hold a feeding territory is ~ 7500 ha. This area is reached at a radius of ~ 12 km from the main roost. At a similar radius, the accumulated area of mudflats around non-roosting locations is on average 1000 ha less, which could hold about 400 fewer feeding territories. Up to 60% of the local Whimbrel population could find feeding territories within 12.5-km radii of the main roost.

Roosting in the centre of the basins with access to more and closer feeding areas could offer a common solution for a larger number of Whimbrels. Our results partially align with the hypothesis of proximity to foraging-patch (Caccamise & Morrison 1988), such that roosts can be understood as the result of birds aggregating near rich sources of food, rather than or in addition to social aggregations *per se*. Raptors (Josens *et al.* 2013, Watts & Turrin 2017), colonial waterbirds (Sparling & Krapu 1994), corvids (Gorenzel & Salmon 1995, Sonerud *et al.* 2001) and other birds and mammals (Beauchamp 2014) form aggregations around food-rich patches. In such cases, roosts are thought to work as 'information centres' and individuals participating could alter their daily behaviour to follow successful foragers. However, Whimbrel territoriality alters the application of this hypothesis; they may occur at higher densities at richer sites but not necessarily alter their foraging behaviour or roosting locations in response to temporal and spatial changes in resource abundance. Rather than aggregate close to richer food sources, roosting aggregations can result from multiple territorial Whimbrels choosing to roost in the vicinity of their territories (Beauchamp 1999).

Alternative feeding habitats and differences in Whimbrel density across the delta could affect estimates of availability of feeding sites around roosts. In the first case, sand beaches and artificial pastures offer foraging opportunities for Whimbrels in Sanquianga (Ruiz-Guerra 2004) but these habitats are scarce and harbour lower bird densities compared with mudflats (Abril 2011). Sand

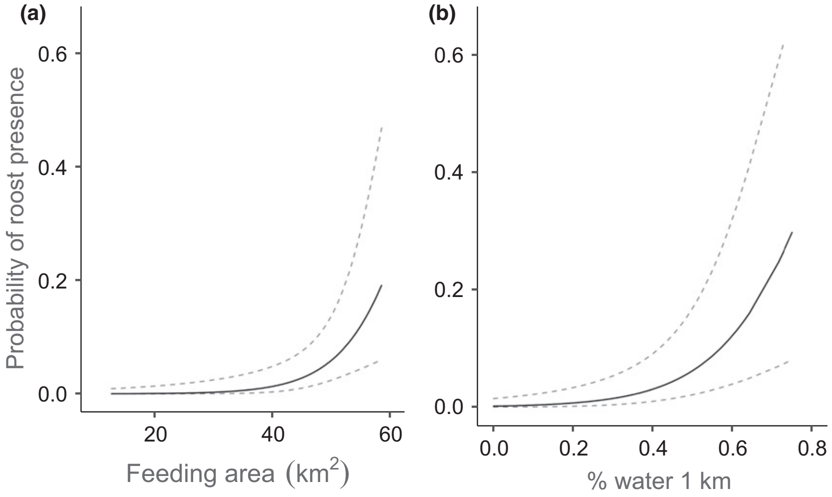

Figure 5. Predicted relationships between the probability of presence of a Whimbrel roost and (a) feeding area within a 12-km buffer and (b) the proportion of water within a 1-km buffer. Hash marks show the raw data and dashed lines indicate the 95% confidence interval for predicted probabilities.

beaches and pastures also occupy a marginal proportion of the habitat (< 2%) in relation to almost 15% of the area occupied by mudflats (UAESPNN 2005). On the other hand, our current estimates of the availability of feeding sites assume an even distribution of Whimbrels across the study area. But broad-scale surveys (Anchico *et al.* 2015) revealed that Whimbrel densities are higher towards the central–west portion of the delta. Whimbrel densities could be associated with differences in profitability of feeding territories. Thus, in addition to a larger availability of mudflats, individual patches near current roosts can harbour more birds. We do not have historical survey data, but we suspect that conditions for Whimbrels and shorebirds in general have changed as compared with 40 years ago when the Patía river was partially diverted into Sanquianga estuary, increasing its volume and sediment load, and doubling the size of mudflats (Restrepo & Kettner 2012, Parra & Ángel 2014). It is likely that the increase in mudflats provides conditions for redistribution of Whimbrels and could have an impact on roost use; however, in the absence of historical survey data, we cannot test this.

Roosting near feeding areas could explain Whimbrel roosting congregations in central sections of Sanquianga but not necessarily the precise islands on which roosts are located. Other mangrove islands close to the roosts are equally or slightly more central than the ones currently used. Furthermore, if access to food were the exclusive driver, Whimbrels would roost adjacent to their territories rather than commute several kilometres to reach the central roosts. Thus, other factors besides feeding site proximity must be involved.

Avoidance of predators

Most of Sanquianga is under tidal influence and the surface permanently above the tide line is very restricted, offering a largely unsuitable habitat for terrestrial predators. Although roosts and other mangrove islands had similar average distances to land, no roosts were located on islands with emerged lands and all were at least 5 km from the mainland. Islands used as roosts by Whimbrels lie on the tail end of the distribution of proportion of water vs. the proportion of mangrove within 1 km of the island. Protection from predators that could reach roost sites by travelling overland could explain this result. In our study area, one extreme example is the cluster of roosts in the middle of the Sanquianga basin, placed in the most isolated locations of the delta, hosting an estimated nearly 95% of observed roosting Whimbrels. By roosting in isolated islands, Whimbrels can potentially reduce their vulnerability to terrestrial predators. This conclusion is consistent with most other studies on roosting shorebirds where they select isolated locations; when barriers to predator movement are weak, this can result in higher shorebird predation (Hockey 1985).

By roosting on islands surrounded by large stretches of water, Whimbrels may gain isolation from predators that could use nearby mangroves to move between islands. Whimbrels arrived at the roost predominantly from southwest and southeast of the park (Hevia 2011), where both a high proportion of feeding habitat is available and individual mudflats are closer to potential sources of predators in the mainland. It is therefore possible that territories near mainland contribute more Whimbrels to the main roost.

The Peregrine Falcon *Falco peregrinus* and domestic cats *Felis silvestris catus* are the only confirmed predators on shorebirds in our study area (Ruiz-Guerra 2004). We have not recorded any predation events for Whimbrel. However, many shorebird predators able to take a Whimbrel are likely to occur in the vicinity of southern Colombian mangroves, including several species of diurnal raptors (Ruiz-Guerra *et al.* 2007, Calderón-Leytón *et al.* 2011), owls (Chaparro-Herrera *et al.* 2015) and a diverse small- to medium-sized mammal community (Ruiz-Guerra *et al.* 2011). Elsewhere, terrestrial mammals are among the main predators of shorebirds at night. For example, mongooses, foxes and other mammals are the main predators of African Oystercatcher *Haematopus moquini* (Hockey 1985). The Whimbrel preference for mangroves as observed in the study area and elsewhere (Zharikov & Milton 2009) contrasts with a predominant use of open roosts found in other shorebirds (Rehfisch *et al.* 2003, Piersma *et al.* 2006, Rogers *et al.* 2006a, Conklin *et al.* 2008). Whimbrel roosting in isolated locations, including mangrove islands (Andres *et al.* 2007), could decrease exposure to terrestrial mammals at night.

Human disturbance

We expected that Whimbrel roosts would be located at greater distances from sources of human disturbance but we found no evidence of this. Whimbrel roosts were closer than other mangrove islands to waterways used for aquatic transportation and distances to villages, and human density around roosts was similar to that of other mangrove islands. An initial interpretation would be that human settlements and shipping activities are not perceived as threats by Whimbrel, but this seems unlikely, given that in other localities this species shows strong responses to both immediate and continued disturbance by humans. For example, Whimbrel show greater flight initiation distances to approaching humans compared with smaller shorebirds (Weston *et al.* 2012) and their selection of roosting sites can be negatively influenced by boat activity (Peters & Otis 2007). Therefore, we interpret our results in two parts: low levels of disturbance in our study area and a non-linear response to avoidance of disturbance. In the first case, although more populated than the average National Park, human settlements are sparse and evenly distributed in Sanquianga (UAESPNN 2005). Nearly 90% of the mangrove islands have no human presence in their immediate proximity (1-km radius) and cargo ships use waterway routes only a few times a day. Compared with shorebird sites close to cities, tourist developments or industrial facilities, where disturbance could limit roost availability (Rogers *et al.* 2006a), human influence in roosts in Sanquianga is probably of low intensity.

Additionally, Whimbrels could select roosting sites not at the maximum distance from human intervention, but rather above a threshold distance. None of the roosts was located on islands containing villages. Similarly, most roosts were at least 1 km away from waterways, but the largest roosts were up to three times further away. Thus, current roosts could be just far enough to avoid major sources of disturbance. We were not able to identify potential thresholds due to the linear, untransformed nature of the variables used to predict the roost location. We did not measure the direct influence of specific disturbance events, but rather the proximity to sources of such disturbances. We do not discard disturbance as an explanation for the location of Whimbrel roosts, but our analysis does not support its importance. Disturbance is regarded as one of the most important threats to populations of Numeniini (Upland Sandpipers *Bartramia longicauda*, Whimbrels, curlews, godwits); however, evidence of its impacts at population level remains uncertain (Pearce-Higgins *et al.* 2017). Although this does not appear to influence current Whimbrel roost locations in our study area, human population growth and increase of fishing activities in the park (UAESPNN 2005) should be monitored to ensure disturbances are not impacting critical sites for roosting Whimbrels.

Do Whimbrels prefer more complex habitats for roosting?

Across their non-breeding range, Whimbrels use a variety of natural and artificial substrates for roosting (Andres *et al.* 2007, Colwell 2010), but in Sanquianga the use of sand spits and beaches occurs mostly diurnally at high tide (Abril 2011, Hevia 2011) or during the pre-migratory periods (R. Johnston-González pers. obs.). In our study area, nocturnal roosting of Whimbrel appears to be limited to mangroves. At other locations with mangroves, Whimbrels also exhibit a preference for this habitat for roosting (Zharikov & Milton 2009). If available, structurally complex habitats such as mangroves could provide additional protection in comparison with open habitats at night, when visual detection of predators could be impaired.

On the advantage of congregating

We have assessed Whimbrel roost locations in relation to habitat features, but social aspects could play a role in the large concentration of Whimbrels at certain sites in our study area. If individuals were making completely independent decisions, we would expect some greater occupancy of other central and isolated islands than we observed. The advantage of the dilution effect (Beauchamp & Ruxton 2008) tapers off with such large numbers. Our surveys are not sufficient to prove that additional roosts do not exist, but our known roosts account for a high proportion of the local feeding population (70–80%) choosing to roost in single or a few islands. To the extent that true social factors contribute to roost formation, they would probably result in the magnification of other effects determining roost location.

CONCLUSION

We contrasted the spatial features of known Whimbrel roosts with all other potential locations available in the mangrove islands of Sanquianga National Park. The location of current roosts was best explained by a combination of access to feeding resources and isolation from potential terrestrial predators. Explanations based on the avoidance of disturbances were not supported by our data. Roosts are situated in central locations, with access to larger areas of mudflats and within close to individual feeding patches. Those roosts were also located on some of the most inaccessible islands in the delta, surrounded by large extensions of water and isolated from other mangroves and non-flooded lands. Whimbrels may perceive these islands as less vulnerable to incursion from terrestrial predators compared with mangroves closer to their feeding territories. Whimbrels may use a simple rule of thumb to reduce predation risk at night: stay away from land that might be used by terrestrial or aerial predators. Current locations provide safe sites while maintaining feeding opportunities within short commuting distances for a larger number of territorial birds that otherwise would use other more peripheral locations.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Proportion of mangrove and water within a 1-km radius of occupied (black) and potential (grey) roost sites. The main roost is indicated by a larger circle.

Table S1. Maximum number of individuals and habitat features of occupied Whimbrel roosts in Sanquianga National Park.

Table S2. Mudflat area (km^2) accumulated around occupied and potential Whimbrel roosting sites in concentric buffers within a 1-km radius. Median, minimum and maximum value and results of Mann–Whitney U-test.